

**Title:** Biogeography and Adaptation in the Kuril Islands, Northeast Asia

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## **Abstract**

The Circumpolar North is generally recognized as a challenging environment to inhabit and yet, we know relatively little about how people managed their welfare in these places. Here, we add to the understanding of maritime hunter-gatherers in the subarctic North Pacific through a comparative approach that synthesizes biogeographic and archaeological data from the Kuril Islands. We conclude that our faunal, ceramic and lithic evidence support biogeographical expectations as assemblages from low biodiversity and insular regions show limited diet breadth, more locally produced pottery and a conservation of lithic resources. However, we highlight that these ecological factors did not strictly determine the occupation history of the archipelago as radiocarbon data suggests all regions experienced similar demographic fluctuations regardless of their biogeography. These results imply additional pressures influenced the strategic use and settlement of the Kuril Islands and the need for increased chronological resolution to disentangle these complex historical factors.

## **1. Introduction**

Maritime hunter-gatherers can be broadly defined as those groups whose subsistence relies primarily on wild resources extracted from the sea. However, given that many northern regions have had only intermittent human presence (Hoffecker 2005; Friesen and Mason 2016) and have been less intensively studied, the archaeological record of Arctic and sub-Arctic maritime hunter-gatherers is often scant. This is unfortunate as the archaeology of northern foragers present valuable opportunities to study long-term interactions between humans and their environments. This is especially true given the challenging climates, inherent instability of high-latitude ecosystems and their reliance on local resources for survival (Damm et al. 2019).

Here, our approach is to compare archaeological and radiocarbon evidence from maritime hunter-gatherers that inhabited a subarctic landscape: the Kuril Islands, an archipelago that stretches from the northernmost Japanese island of Hokkaido to the southern tip of the Kamchatka peninsula (see Fig 1). We start from the well-established premise that islands make good areas for studying historical hunter-gatherer relationships to ecological variability (Keegan

and Diamond 1987; Vitousek 2002; Fitzpatrick and Keegan 2007; Kirch et al. 2007; Rick 2007; Braje et al. 2017; DiNapoli and Morrison 2017; DiNapoli and Leppard 2018). This is not because hunter-gatherer behaviors are determined in any simple sense by geography, but because differences within island chains structure differences in the character of environmental challenges that settlers had to manage strategically and often socially (Fitzhugh and Hunt 1997; Lape 2004; Lawson et al. 2005; Fitzpatrick and Anderson 2008; Fitzhugh, Phillips, and Gjesfeld 2011; Hudson, Aoyama, and Hoover 2012; Leppard 2015; Giovas 2016).

The analyses presented here follow predictions drawn from biogeographical principles predicting the vulnerability of populations based on their geographical and ecological circumstances related to island contexts (Fitzhugh and Hunt 1997; Brown and Lomolino 2000; Steadman 2006). Brown and Lomolino (2000) show how simplistic biogeographical predictions do not apply cleanly or linearly in biology. In addition to simple distances (dispersal filter) and area (habitat availability/heterogeneity) relationships, factors such as the dispersal ability and migratory range of taxa, their reproductive rates, habitat requirements, tolerance for seasonal variability, degree of generalist versus specialist adaptations are all important factors in local ecological diversity and resilience. As Fitzpatrick and colleagues (2007) observe, biological and archaeological research has successfully challenged the more deterministic ecological predictions of early island biogeography expectations without undercutting the more general utility of the approach. The early models, applied both to human and non-human populations, took too little account of variations in physical, biological, and cultural characteristics such as ocean currents, climatic conditions, dispersal abilities, energetic needs, and for humans, such considerations as seafaring technologies, political organization, and beliefs.

We use the principles of island biogeography in this study for heuristic and comparative purposes under the assumption that human, like other species, face increased risks of starvation and population decline or extinction when confronted with periodic and unpredictable subsistence failure that they are unable to mitigate through diversification, storage, mobility, or trade. All else being equal, remote islands present more limited opportunities for colonization and small islands have fewer habitats to support taxonomic diversity. As a result, islands that are both small (or more precisely, that have more limited habitat area to support biotic production and diversity—terrestrially and/or in surrounding marine zones) and far from the source of biotic replacement are more hazardous for settlement by hunter-gatherers who depend on locally available flora and fauna for their livelihoods. While humans develop a range of strategies to overcome these risks, they are not immune to them, and archaeological evidence should provide a window through which to examine how people managed these risks and how they sometimes failed to do so.

These principles lead to a range of archaeological expectations for the histories of hunter-gatherer groups settling islands of varying geographic and ecological characteristics. For example, one can expect settlement to occur sooner on less remote islands. More remote settlement, especially on smaller islands (islands of reduced habitat and productivity), should be limited to those equipped to invest in more intensive production, higher mobility, or more social and economic networking over longer distances. Social networks are particularly important where local populations are small so as to maintain sufficient access to marriage partners and to compensate for the greater risk of relying on vulnerable (low diversity) local ecosystems. Larger

islands (larger habitats), in general, should support more sustainable settlement, while small and remote islands might be abandoned and reoccupied more frequently.

We build from this foundation to address three key questions using previously unreported analyses of zooarchaeological, artifactual, and radiocarbon evidence:

- How mobile were populations living in the Kuril Islands?
- Do biogeographical and ecological differences relate to regional differences in the occupation and cultural history of the archipelago?
- Do more remote and ecologically precarious islands show more punctuated occupation histories compared to others?

Broadly speaking, we see these questions as helping to evaluate the extent to which the settlement of the Kuril Islands was a risky prospect for small, maritime hunting and gathering communities. We attempt to answer these questions in part by evaluating the degree of human resilience documented by archaeological continuity in comparison with regional differences in remoteness, access to outside/mainland resources and networks, biogeographic richness and abundance. Furthermore, we anticipate that hunter-gatherer peoples commonly develop effective strategies for mitigating environmental risks through the diversity of their harvesting practices, logistical and residential mobility, and the intensity and structure of their social networks. Here, we report the results of zooarchaeological and artifact analyses relevant to addressing these questions and to a broader understanding of how maritime hunter-gatherers managed the challenges of subarctic landscapes.

## **2. The Kuril Islands**

The Kuril archipelago is a volcanic island arc consisting of approximately 32 islands that stretch from the island of Hokkaido, Japan to the Kamchatka peninsula, Russia. From 2006 to 2010, this chain of islands was the focus of Kuril Biocomplexity Project (KBP) field research, which broadly aimed to explore the history of occupation and interaction within the context of a remote, island region (Fitzhugh 2018). Building from a human ecodynamics foundation, KBP developed a multidisciplinary understanding of how changes in socio-ecological systems altered the stability and resilience of Kuril human populations in the past. The broad methodological scope of the project incorporated experts in marine geology, volcanology, paleoclimatology, paleobotany, and archaeology. The research presented here also builds from archaeological work performed in 2000 in collaboration with the International Kuril Islands Project (IKIP) as well as the more recent Kuril Ainu Archaeological Project (KAAP).

Some of the most significant features of the Kuril archipelago are the dramatic differences in both terrestrial and aquatic/marine biogeography between islands at the ends and center of the archipelago (see Fig 1). Due to a combination of larger landmass and closer proximity to Hokkaido, the southern islands maintain a much higher level of biodiversity (Pietsch et al. 2003). This includes many different types of trees and shrubs (Anderson et al. 2008), insects, mollusks, and fish (including anadromous salmonids) (Pietsch et al. 2001; Pietsch et al. 2003; Fitzhugh et al. 2016) and terrestrial mammals including bears, hares, weasels and rodents (Hoekstra and Fagan 1998). Likewise, Paramushir and Shumshu in the north have occasional large terrestrial

animals that swim over from Kamchatka and large enough rivers to support anadromous salmonid populations. The islands at the ends of the archipelago are also large enough to develop a diverse range of intertidal and benthic communities and a greater variety of marine animals that feed on them. In contrast, the islands in the central part of the archipelago have relatively depauperate terrestrial ecosystems (Hoekstra and Fagan 1998; Pietsch et al. 2003) and lack anadromous fish streams/rivers.

#### INSERT FIGURE 1

Fig 1. Map of Kuril Islands showing major islands and biogeographic regions discussed in the text with major straits labeled with dashed lines (Map is redrawn from a base-map by Adam Freeburg and adapted from Fitzhugh et al. 2016).

To facilitate our comparative approach, we partition the Kuril Islands into four regions: South, South-central, North-central and North (see Fig 1). The boundaries between these regions are largely based on the biogeographical differences highlighted above. The South region includes islands up to the Bussol Strait and is characterized by greater biodiversity and closer proximity to Hokkaido. The South-central and North-central regions extend north from the Bussol Strait to the strait that separates the islands of Onekotan and Paramushir (occasionally referred to as the “Fourth Strait”). These islands, also referred to as the “remote islands” (Gjesfjeld 2019), are substantially smaller in size, maintain much lower biodiversity and are more geographically isolated. The North region is largely comprised of the islands of Paramushir and Shumshu, which has higher biodiversity than the South-central and North-central regions, but lower than the South region.

The geographic configuration of the Kuril Islands, in combination with varying local ecologies, provides a unique opportunity to explore the influence of biogeography on the human occupation of the region. Our starting expectations suggest that settlement of large islands with greater biodiversity and that are closer to the population centers of Hokkaido and Kamchatka should have higher rates of immigration and a greater degree of archaeological and faunal diversity (Fitzhugh et al. 2004). Conversely, smaller islands farthest from source areas with lower biodiversity are viewed as being more precarious and likely to have lower archaeological and faunal diversity, as well as higher rates of both population immigration and extinction.

The earliest evidence of human occupation in the Kuril Islands dates to around 8000-7600 calBP and can be found at the Yankito site complex on the southern island of Iturup (Yanshina and Kuzmin 2010; Kuzmin et al. 2012). The northernmost island of Shumshu also appears to have been settled, at least intermittently by 6000 years ago, probably from Kamchatka, by crossing the relatively narrow First Kuril Strait (Fitzhugh et al. 2016; Takase et al. 2017). The first prolonged occupation of the more remote islands north of the Bussol strait and south of Shumshu is associated with the Late/Final Jomon and early Epi-Jomon cultural phases as defined in Hokkaido (Fitzhugh et al. 2016). The more intensive occupation of the remote islands (up to Shiashkotan Island) by Epi-Jomon populations is particularly notable, as this culture is commonly recognized as an extension of Jomon hunter-gatherer culture (from the south) but with greater intensification on marine mammals and improved harpoon technology (Okada 1998; Fitzhugh et al. 2016). The Epi-Jomon culture of Hokkaido was quite different in subsistence and

settlement patterns to the earlier Jomon period (Takase 2014). In the Kuril Islands, Epi-Jomon settlements are characterized by relatively small, single-room house pits (approximately 15-30 m<sup>2</sup>) often situated in larger multi-component sites (Fitzhugh 2019; Fitzhugh et al. 2016). Evidence for this initial population pulse is clearly recognized in an island-wide paleodemography model, where the density of calibrated radiocarbon dates increases substantially during the Late/Final Jomon and early Epi-Jomon period (Fig 2).

A second major observation from the paleodemography model is the strong pattern of population “booms and busts” with increases in population density followed by declines. This pattern is not only recognized during the Epi-Jomon period (2400-1300 calBP), but is repeated with even greater intensity during the later Okhotsk cultural period (1300-700 calBP). The Okhotsk culture is recognized as a distinct culture from the preceding Epi-Jomon culture. The Okhotsk originated in the western Sea of Okhotsk around the Soya Strait, in the vicinity of southern Sakhalin and northern Hokkaido (Amano 1979; Sato et al. 2007; Deryugin 2008). Archaeological sites associated with the Okhotsk culture can be found throughout the Sea of Okhotsk coast from Sakhalin to the Kurils occasionally displaying large houses and fortified settlements (*chasi*), although no *chasi* were definitively identified in the remote Kuril Islands (Fitzhugh et al. 2016; but also see Takase et al. 2017; Fitzhugh 2019). The Okhotsk occupation of the Kuril Islands, particularly the North-central region, is intensive but short-lived with a dramatic decline in radiocarbon dates and artifacts around 700 calBP. It is now believed that the later Ainu culture is the result of assimilation between Okhotsk population and Jomon-descendent Satsumon communities (Tobinitai culture) across southern and eastern Hokkaido (Hudson 1999; 2004). The Ainu culture eventually spreads throughout Hokkaido and into the Kuril Islands and southern Kamchatka (Torii 1919; Takase 2013) with ethnohistorical evidence suggesting the Kuril Ainu developed a unique subculture with distinct dialects and practices (Snow 1897; Krashennnikov 1972; Fitzhugh et al. 2016).

INSERT FIGURE 2

Fig 2. Temporal frequency distribution of calibrated radiocarbon probabilities from 364 dates from Kuril archaeological sites (redrawn from Fitzhugh et al. 2016). In addition, approximate dates for cultural periods identified in the Kuril Islands. Solid black line represents a kernel density estimate (KDE) and grey line indicates the summed probability distribution (SPD).

### 3. Comparison of Archaeological Remains and Radiocarbon Data

The data presented here comes from archaeological survey conducted by the KBP, the earlier International Kuril Islands Project (IKIP), and the subsequent Kuril Ainu Archaeological Project (KAAP). In total, these projects recorded 110 archaeological sites on 16 of the largest islands in the Kuril archipelago (Fitzhugh 2019). It should be noted that less archaeological work has taken place in the North region and therefore insights into the occupation of this region should be considered preliminary.

#### 3.1 Faunal Remains

All of the faunal data presented here was excavated by various KBP research teams from 2006-2008. Multiple excavation units (typically 1 m x 1 m, but occasionally 2 m x 2 m) were situated in areas either known from surface examination to contain preserved midden deposits or suspected due to their proximity to surface features of semi-subterranean house pits (Fitzhugh et al. 2007; Fitzhugh, Phillips, et al. 2009; Fitzhugh, Etnier, et al. 2009). Excavated faunal materials were water-screened through 6.4 mm (1/4") screens with 3.2 mm (1/8") fractions systematically saved for future analysis. Samples from the 3.2 mm fraction were examined for evidence of small-bodied fish such as herring (*Clupea pallasii*) and sardine (*Sardinops sagax*). Only remains from the larger (6.4 mm) screens are reported here, but we note that no herring or sardines were encountered in either the larger or smaller screen fractions in any of the four assemblages. If small-bodied fish species are present in our samples our results may be partially impacted (Butler 1993; Partlow 2006); however, our assemblages are clearly dominated by cod (*Gadidae*) or greenling (*Hexagrammidae*) so diversity indices are unlikely to change significantly. Bulk midden samples from KBP excavations are retained at the Burke Museum of Natural History and Culture in Seattle, WA.

Birds and mammals were analyzed in their entirety, while invertebrate and fish remains were sub-sampled with different quantification methods used depending on the taxonomic group under consideration. The number of urchins (*Strongylocentrotus* spp.) in each assemblage was documented by counting the number of mouthparts present (demipyrramids from the "Aristotle's lantern"). Gastropods were quantified using minimum number of individuals (MNI), based either on whole bivalves or relatively complete spires. Bivalves were quantified with the number of identified specimens (NISP) using only hinges. Finally, fish, birds, and mammals were quantified using NISP (but ribs, vertebrae, and phalanges of birds and fish were not identified above the level of Class).

Throughout the Kurils, the most abundant archaeofauna encountered came from archaeological contexts attributable to the Okhotsk occupation phase of approximately 1,200 and 700 calBP (by either date or association with diagnostic artifacts). In the rare cases where we discovered fauna from earlier or later phases, the deposits were disturbed in such a way that chronological separation was not possible. This is especially the case for the organically well-preserved site of Ainu Creek on Urup Island, which had Epi-Jomon and Okhotsk components that were mixed by road building activities between our visit in 2006 and the excavations of our Russian colleagues in July 2007. With this and a few other minor exceptions, the regional patterns discussed here should relate primarily to the lifeways of Okhotsk period settlement. The inability to track change in faunal use through time and across the archipelago was an unexpected and disappointing element of the KBP research effort.

Fauna was regularly preserved only where shells were present and therefore it is not surprising that our collections include many invertebrate shell remains. It is difficult to compare the relative abundance of urchins to other invertebrate taxa in any meaningful way, but note that urchin remains were present in sites from all of the four regions (see Table S1 in the supplemental information). With the exception of minor amounts of mussel (*Mytilus* sp.) in sites from the South-central, North-central, and North regions, bivalves are only present in sites from the north region. However, sites from all regions had abundant gastropod remains, primarily periwinkle (*Littorina* sp.) with lower, but consistent amounts of various whelk species (*Buccinum* sp. and

*Nucella* spp.) (Table S1 in supplemental information). In fact, during excavations of shell midden deposits our team encountered lenses of nearly pure urchin tests (body fragments) or periwinkle shells. A source of considerable speculation among our team, we have yet to derive a reasonable explanation for the near absence of bivalves from the South or remote island regions.

The geographic patterning of fish remains is even more striking than the patterning of the invertebrate remains. In the south, a high diversity of fish was targeted, including sharks (*Lamnidae*), salmonids (*Salmonidae*), sculpins (*Cottidae*), greenlings (*Hexagrammidae*) and cod (*Gadidae*). Three of these groups (sculpins, greenlings, and cod) made significant (defined here as  $\geq 10\%$  of the overall NISP for that Class) contributions to the assemblage. In the South-central region, the fish assemblage is dominated by greenlings to the near exclusion of all other taxa. Sites in the North-central region were specifically targeting cod, perhaps as part of a seasonal procurement system. Finally, sites in the north region are uniquely focused on salmon and cod (see Table 1 below).

<b>Taxonomic Group</b>	<b>South</b>	<b>South-central</b>	<b>North-central</b>	<b>North</b>
Gastropods	1423 (100.0)	8382 (99.8)	4790 (99.3)	2212 (78.1)
Bivalves	-	20 (0.2)	33 (0.7)	621 (21.9)
ALL INVERBRATES	1423	8402	4823	2833
Sharks	15 (2.9)	1 (0.0)	-	-
Salmon	7 (1.3)	24 (0.7)	-	907 (54.3)
Sculpins	227 (43.2)	6 (0.2)	4 (0.3)	2 (0.1)
Greenlings	212 (40.3)	3515 (99.1)	112 (8.2)	31 (1.9)
Cod	65 (12.4)	1 (0.0)	1247 (91.5)	666 (39.9)
Flatfish	-	-	-	65 (3.9)
ALL FISH	526	3547	1363	1671
Loons, Grebs	14 (1.1)	2 (0.0)	5 (1.6)	5 (3.3)
Albatrosses	314 (25.3)	1262 (24.0)	6 (2.0)	2 (1.3)
Tubenouts	70 (5.6)	609 (11.6)	97 (31.8)	-
Cormorants	309 (24.9)	179 (3.4)	64 (21.0)	76 (50.3)
Auklets, Puffins, Murres	136 (11.0)	2807 (53.4)	59 (19.3)	18 (11.9)
Ducks, Geese Swans	42 (3.4)	232 (4.4)	33 (10.8)	26 (17.2)
Gulls	39 (3.1)	66 (1.3)	9 (3.0)	21 (13.9)
Raptors	312 (25.1)	72 (1.4)	10 (3.3)	-
Songbirds	5 (0.4)	23 (0.4)	11 (3.6)	3 (2.0)
Ptarmigan	-	-	11 (3.6)	-
ALL BIRDS	1241	5252	305	151
Dogs, Foxes	74 (2.8)	70 (10.0)	37 (16.9)	6 (4.3)
Other Carnivores	218 (8.3)	34 (4.8)	15 (6.8)	31 (22.0)
Fur seals, Sea lions	289 (11.0)	216 (30.7)	93 (42.5)	31 (22.0)
True seals	487 (18.6)	287 (40.8)	49 (22.4)	61 (43.3)
Artiodactyls	9 (0.3)	1 (0.1)	-	-
Dolphins, Porpoises	970 (37.0)	16 (2.3)	-	-
Other Cetaceans	578 (22.0)	79 (11.2)	25 (11.4)	12 (8.5)
ALL MAMMALS	2625	703	219	141

Table 1. Table recording the number of identified specimens (NISP) for key taxonomic groups organized by region. Values in parentheses indicate the relative proportion of each taxonomic group to their class totals. Additional details including species identifications and the number of unanalyzed and unidentified specimens can be found in Table S1 in the supplemental information.

Bird remains are slightly less geographically patterned than the fish remains, but nevertheless still show some significant patterning (Table 1). For instance, only one region, the South, had a significant contribution of raptors. Albatross (*Phoebastria*) were only significant in the South and South-central region, whereas gulls (*Larus*; *Rissa*) were significantly represented only in the archaeofaunas from the North region. Alcids (*Alcidae*), including auklets, puffins, and murres as well as cormorants (*Phalacrocorax*) are nearly ubiquitous in archaeological assemblages throughout the archipelago, but the Procellariids (also called “tubesnouts”) are restricted to the South-central and North-central regions. Note that the specimens identified as “cf. *Fulmarus glacialis*” or “most likely to be northern fulmar” (see Table S1) are all from juveniles, indicating that nearby breeding colonies were being targeted for at least part of the year.

Not surprisingly, marine mammals were harvested throughout the Kuril Islands. However, data from the middens show that the situation is nuanced. For instance, although Otariids (fur seals and seal lions) and Phocids (harbor seals, largha seals, and ringed seals) made significant contributions in all four regions (Table 1), the overall relative abundance of Otariids was higher in the more insular South-central and North-central regions. And although Cetaceans (whales and dolphins) were utilized throughout the archipelago, it is only in the South region that dolphins (*Delphinidae*) contribute significantly. Finally, and most counter-intuitive, terrestrial mammals are most significant to the overall mammal assemblage in the South-central and North-central regions—regions where terrestrial mammal assemblages have the lowest biodiversity (Hoekstra and Fagan 1998). This pattern is driven nearly exclusively by the presence of domestic dogs (*Canis familiaris*) and red foxes (*Vulpes vulpes*). The remains of dogs and foxes were found in undistributed midden contexts and initially interpreted as being food remains, but other uses for these animals are plausible (hunting, protection, furs, etc.). Exactly how the bones of red foxes ended up in prehistoric midden deposits is currently unknown, especially in the remote islands of the archipelago. Prehistoric introduction of foxes into island systems has been documented elsewhere (Rick et al. 2009) and cannot be ruled out in the Kuril Islands. A full analysis of the fox remains including aDNA, isotopes, and direct radiocarbon dating is forthcoming (Etnier et al. in prep)

The taxonomic richness of the faunal assemblage shows a general similarity between the number of taxa exploited in the South (39), South-central (43), North-Central (36), and North (35). However, this pattern can be deceptive. When differences in evenness (i.e. the abundances of each taxa) are accounted for, the diversity is lower in the South-central and North-central regions (see Figure 3). This suggests a narrower diet breadth of populations in these regions with a concentration on only a handful of taxa (greenling, puffin, cod). This is consistent with the patterns previously identified in a smaller study of faunal remains from the islands of Chirpoi and Shumshu (Fitzhugh et al. 2004).

INSERT FIGURE 3



Figure 3. Barplot of richness (number of taxa) by region for faunal remains that could be identified to their taxonomic group. The width of bars indicates the proportion of each taxonomic groups NISP to the total NISP of the regional assemblage (n). A Shannon-Weaver diversity index (Shannon and Weaver 1948) indicated as  $H'$  is also included for each region, which provides a measure of diversity accounting for both the richness and evenness of the faunal assemblages.

### 3.2 Lithic Artifacts

We evaluated the degree of lithic management in the Kuril Islands through the examination of size, use and knapping technique of flakes. Our starting expectation was that the size and use of flakes should be related to the abundance of lithic raw materials in each region as it is reasonable to expect that smaller raw materials are more often used on remote islands due to the relative paucity of lithic raw materials available there. Furthermore, the occurrence of pressure flaking should be higher on smaller and insular islands as tools will be retouched and resharpended repeatedly to use lithic materials more efficiently.

In the Kuril Islands, local raw materials such as basalt, chert, shale, and chalcedony were mainly used for producing stone tools. Earlier studies, based on primarily undated surface collections, found that although obsidian as a non-local material was also used, its occurrence is constantly lower than local materials (Fitzhugh et al. 2004; Phillips and Speakman 2009). Analyses of the cortex, size, striking platform, and flake scars of debitage in the IKIP collection indicate that lithics from the Kurils were more intensively worked and curated compared to materials from Sakhalin (Fitzhugh et al. 2004). This suggests that predictions based on island biogeography are generally supported; local raw lithic materials are limited on smaller insular islands.

A similar tendency can be seen in the larger collection obtained by KBP for which we present new results here. Like earlier studies, these findings are limited in chronological discrimination by their collection context. Despite the large number of radiocarbon dates generated by KBP (discussed below), artifacts included in this analysis derive from a much larger number of excavation and surface collection contexts, mostly without clear cultural diagnostics or dates. Use of the full data set for geographically robust comparisons necessarily masks temporal variability within sites and regions. Future analyses will explore chronological aspects of these patterns to the extent possible with these data, while additional archaeological excavation and expansion of well-dated assemblages throughout the archipelago is needed. We anticipate that realizing that goal will likely take years if not decades of additional research.

Turning to the patterns seen in KBP lithic data sets, we sought to evaluate the patterns seen previously that suggest technology was influenced by island insularity and size. Here we report on flake size and the utilization of larger flakes by island region as a proxy for conservation of toolstone. The frequency of relatively large flakes ( $> 4$  cm) from South-central and North-central regions is lower than those from the South and the North, indicating that larger cores were more limited in insular small islands (Table 2). Large flakes are useful not only for making formal stone tools but for various temporary uses. If they were intensively curated, a greater percentage of large flakes should have been utilized not to waste lithic raw materials. However, the ratio of

utilized large flakes (large flakes with micro-flakings generated by use) is very low in the South-central region. In contrast, the percentage of utilized large flakes to all large flakes is high (21.7 %) in North-central, suggesting that lithic raw materials were more intensively curated in North-central than South-central region.

Region	Total weight (g)	Count of large flakes (> 4 cm)	Percentage of large flakes (per 1,000g)	Count of utilized large flakes	Percentage of utilized large flakes to total large flakes
South	63463.4	1318	20.8 %	109	8.3 %
South-central	22015.2	257	11.7 %	3	1.2 %
North-central	15026.8	161	10.7 %	35	21.7 %
North	5857.0	78	13.3 %	7	9.0%
<b>Total</b>	<b>106362.4</b>	<b>1814</b>	<b>17.1 %</b>	<b>154</b>	<b>8.5 %</b>

Table 2. Raw counts and occurrence of large flakes (> 4 cm) made of local raw materials and large flakes with micro-flakings.

We applied high-power magnification to examine use-wear and reveal the degree of lithic raw material curation and the purpose of flake use (Keeley 1982). Use-wear polish was detected on 17 specimens of 154 retouched flakes (11.0 %). ‘Dry-hide polish’ (Keeley 1982) could be seen on 16 of those specimens, while ‘wood polish’ was discovered on the remaining, single specimen, suggesting that utilized large flakes were mainly used for hide-working (Fig 4). Notably, almost all of the utilized large flakes (16 specimens) with use-wear polish were from the South region; only a single specimen with ‘dry-hide polish’ was discovered from the North. Additionally, no heavily developed use-wear polish was discovered in any of the lithic materials. Thus, large flakes were actively produced in the South and frequently used for processing hide in the region, but they were likely to be expedient tools. However, we could not reveal the use of large flakes in the South-central and North-central regions. Although large pieces of lithic raw material were more difficult for prehistoric people to obtain in both the South-central and North-central islands, there were differences. Apparently, people living in the South-central islands had more access to large flake cores and could afford to discard large flakes more frequently. Raw materials were more heavily curated in the North-central islands resulting in high frequencies of utilized large flakes. Whether this was because of more limited access to large nodules in local raw materials or to more intensive reduction of imported raw materials we cannot yet resolve.

INSERT FIGURE 4

Fig 4. Use-wear polish observed on flakes from the Ainu Creek 1 site (taken by a digital camera Wraymer NT1000 mounted on a metallurgical microscope Olympus BX-FM). The width of each picture is approximately 900  $\mu$ m.

Although the Kuril Islands are volcanic in origin, there is no high-quality obsidian available for making stone tools in the archipelago itself. Instead, obsidian was imported into the Kuril Islands from Hokkaido and Kamchatka (Kuzmin, Glascock, and Sato 2002; Kuzmin and Glascock 2007; Kuzmin et al. 2008; Phillips and Speakman 2009; Phillips 2010; Kuzmin 2012). Figure 5 shows

the relationship between obsidian debitage size and crack velocity estimated using an angle formed by fracture wings as seen in Figure 6 (Tomenchuk 1985; Hutchings 1999). Estimated crack velocity is classified into three groups related to the knapping technique (Takakura and Izuho 2004). Group I (< 500 m/s) has a strong correlation with pressure flaking, and Group II (500-900 m/s) is closely related to indirect percussion with hard hammers or direct percussion with soft hammers. Finally, Group III (900 m/s) represents direct percussion with hard hammers. The size of obsidian debitage from the Kuril Islands tends to be smaller than that from southern Kamchatka and the number of obsidian flakes from the South-central and North-central is much smaller than other regions. Also, pressure flaking (Group I) was more frequently used in the Kuril Islands compared to Kamchatka, the difference in flake size is not very large between groups in the South-central and North-central islands. This indicates that smaller obsidian raw materials were carried into the Kuril Islands and were more intensively curated in the South-central and North-central regions. Although some large flakes made of local materials were an expedient tool for processing hide, obsidian was used as a valuable lithic raw material throughout the Epi-Jomon and the Okhotsk cultures.

INSERT FIGURE 5

Fig 5. Relationship between obsidian flake size and the crack velocity estimated based on the fracture wings. Groups I-III indicate the classification of crack velocity; Group I: < 500 m/s; Group II: 500-900 m/s; Group III: > 900 m/s.

INSERT FIGURE 6

Fig 6. Examples of observed fracture wings from the sites of Vodopadnaya 2 (left) and Ainu Creek 1 (right). The width of each picture is approximately 900  $\mu$ m.

In summary, the lithic remains collected from the KBP project reinforces and expands the patterns observed in earlier analysis (Fitzhugh et al. 2004) showing that the central islands had more limited access to large cores and high-quality raw materials, especially obsidian. The addition of micro-wear and microscopic fracture analyses adds additional insights about the function of flake tools and the nature of lithic tool production in these islands.

### 3.3 Pottery

The analysis of ceramic remains, based on previous work by Gjesfjeld (2014), has two primary goals. The first is to broadly identify the cultural history of each region and the second is to infer the relative proportion of pottery produced non-locally. Sampling of the ceramic assemblage recovered by KBP proceeded by first selecting sherds that displayed decorative and diagnostic features, then undecorated sherds that could be identified as a part of the vessel rim or base, and finally a random sample of the remaining plain body sherds (see table 3). It is important to note that Epi-Jomon sherds commonly display cord-marking decoration making them easier to identify and assign a cultural affiliation. Okhotsk sherds will not as often display diagnostic features and therefore a significant portion of unassigned pottery sherds are likely affiliated with the Okhotsk culture. Wall and base thickness between Epi-Jomon and Okhotsk sherds are

significantly different from each other (Gjesfjeld 2019) and were generally used as further criteria for assigning cultural affiliation where other diagnostic attributes were absent.

Region	N	n	Count of diagnostic sherds	Count of sherds identified as Epi-Jomon	Count of sherds identified as Okhotsk
South*	2203	682	317	271	46
South-central	1908	357	161	133	28
North-central	201	62	21	9	12
North	32	14	1	0	1
<b>Totals</b>	<b>4344</b>	<b>1115</b>	<b>500</b>	<b>413</b>	<b>87</b>

Table 3. Comparison of pottery sherds from regions of the Kuril Islands including the total number of sherds recovered from KBP (N), the number of sherds sampled from each region (n), the count of diagnostic sherds selected for analysis, and the number of diagnostic sherds assigned to either the Epi-Jomon or Okhotsk cultures (the few remaining diagnostic sherds were assigned to either Jomon or Naiji). \*The exact number of sherds from the Ainu Creek 1 site is unknown and so an estimate of 1000 sherds was used here.

Diagnostic ceramics from all three regions indicate definitive occupation by both Epi-Jomon and Okhotsk populations. Pottery associated with the Epi-Jomon culture is prevalent throughout the archipelago with diagnostic pottery found as far north as the site of Drobnyye 1 on the island of Shiashkotan in the North-central region, see Fig 7. The overall trend is that ceramic assemblages from the South and South-central regions display fairly similar proportions of diagnostic pottery associated with the Epi-Jomon and Okhotsk cultures, suggesting a fairly strong connection between the occupation histories of the two regions. The ceramic assemblage from the North-central region highlights a stronger Okhotsk presence given the high proportion of sherds diagnostic of Okhotsk-style pottery. It is important to note that pottery associated with the Middle, Late and Final Jomon periods are found in the South islands and described in further detail in the appendix of Fitzhugh et al. (2007). Two sherds associated with the Tobinitai pottery tradition were also found at the Olya I site located in the South region, but none were found further north. A handful of Ainu (Naiji) pottery was also found through surface and test pit surveying in the South-central and North-central regions (Fitzhugh et al. 2007; Fitzhugh, Phillips, et al. 2009; Fitzhugh, Etnier, et al. 2009) and are well established on southern Kamchatka (Takase 2013; Takase and Lebedintsev 2016; Takase and Lebedintsev 2019). Given the limited amounts of Tobinitai and Naiji pottery found during KBP excavations, they are not included in analysis performed below, and these archaeological cultures are assumed not to have contributed significantly to the patterns discussed here for fauna, lithic or pottery.

INSERT FIGURE 7

Fig 7. Selection of Epi-Jomon and Okhotsk ceramics from the South (top), South-central (middle) and North-central (bottom) regions. SM# refers to the Sakhalin Museum accession number (if available) and FS# refers to the KBP field specimen number.

The relative proportion of pottery produced on each island was estimated using results from the geochemical compositional analysis of ceramic artifacts (Gjesfjeld 2018). Here, we use compositional data on ceramic artifacts collected through the bulk analysis of 279 pottery sherds using inductively coupled plasma-mass spectrometry (as outlined in Gjesfjeld 2018). Islands were chosen as the unit of analysis as it is expected that the geochemistry of each island is more similar to itself than to other islands, particularly those located in different regions. Islands that had fewer than 15 total samples were not included in this analysis due to statistical concerns when using fewer observations (sherds) than variables (elements).

The determination of island or off-island ceramic production was accomplished using a robust outlier detection algorithm implemented in the robCompositions package (Templ, Hron, and Filzmoser 2011), available in the R statistical environment (R Core Team 2019). This algorithm (outCoDa) calculates Mahalanobis distances from transformed compositional values in order to identify a majority of compositional values from each island. A threshold value, similar to a significance level, is then used to determine the ceramic sherds from each island that are most likely to be compositional outliers (Templ, Hron, and Filzmoser 2011).

Results of the outlier detection analysis indicate a majority of pottery sherds recovered from the same island have similar geochemical compositions. The South islands of Iturup and Urup have the greatest proportion of geochemical outliers, whereas the islands of Rasshua and Shiashkotan in the North-central and South-central regions have the lowest proportion (see Fig 8). These results are generally reflective of island size with larger numbers of raw clay sources and greater geochemical variability most likely on the larger islands in the South. Overall, the geochemical analysis suggest that most pottery was produced, used, and discarded on the same island as recovered archaeologically, strengthening previous results reported at the site level (Gjesfjeld 2014).

INSERT FIGURE 8

Fig 8. Results of outlier detection on geochemical data from pottery samples. Percentages represent the proportion of samples that are considered outliers based on a 95% significance level. The dashed line indicates the Mahalanobis distance threshold value based on the use of 16 elements chosen for their discrimination properties.

### 3.4 Radiocarbon Dates

Over the last two decades, archaeology has witnessed a dramatic rise in the aggregation, quantification and interpretation of radiocarbon datasets. Extending from a “dates as data” approach (Rick 1987), radiocarbon data are used to estimate the density and distribution of occupation aggregated over any number of archaeological sites or regions. This approach is affected by sample size, differential preservation, and uneven sampling of archaeological deposits (MacInnes, Fitzhugh, and Holman 2014; Fitzhugh et al. 2016; Brown 2017). The methods used for constructing population changes derive from recent statistical advancements in modeling radiocarbon dates (Crema 2012; Brown 2015; Brown 2017; Crema et al. 2017). Broadly speaking, the summed probability distributions (SPDs) are the aggregation of all the calibrated radiocarbon dates from each region. The composite kernel density estimate (KDE)

provides a smoothed version of the SPD using randomly sampled calendar dates, with additional details discussed by Brown (2017). An island-wide model of Kuril population dynamics was developed using a series of protocols to control for various biases (Fitzhugh et al. 2016), and here we use the same approach for investigating the population dynamics within each region of the Kuril Islands.

The paleo-demographic models of the Kurils by region (see Fig 9) broadly parallel population trends seen in the aggregated, island-wide model (Fig 2). The South and South-central regions both show an initial rise and fall in population density between 3000 to 1500 calBP and a second rise and fall in population density from 1500 calBP to 550 calBP. These trends are consistent with diagnostic archaeological data, specifically pottery remains, which also suggest occupation of these regions during the Epi-Jomon (2400-1300 calBP) and Okhotsk (1300-700 calBP) periods. The North-central region shows a somewhat different population trend with a much less apparent population increase through the Jomon and Epi-Jomon phases (3000 to 1300 calBP). The Okhotsk population surge and subsequent collapse is represented in the North-central region between 1200 calBP to 550 calBP, similar to the islands to the south. The North region has only 32 radiocarbon dates, which was considered too few to produce a reliable SPD. Once again, this estimate of population density is consistent with archaeological remains that suggest the widespread presence of the Okhotsk culture in the islands of the North-central region.

INSERT FIGURE 9

Fig 9. Summed probability distributions and composite kernel density estimates for the South, South-central and North-central regions. Radiocarbon dates come from Fitzhugh et al. (2016) with analytical functions implemented using the rcarbon package (Bevan and Crema 2018) available in the R statistical environment (R Core Team 2019).

## 4. Discussion

### 4.1 How mobile were populations living in the Kuril Islands?

Anthropologists have long recognized the importance of mobility on hunter-gatherer lifeways (Kelly 2013), and while many hunter-gatherer groups are mobile, there is substantial variation in how and when groups move. The Kuril Islands offer a unique perspective on hunter-gatherer mobility as resources are unequally distributed with some islands having significantly higher diversity or abundances of resources. Furthermore, the geography of the island chain limits the movement between regions due to the presence of large open-water straits that can be difficult to navigate (Etter 1949; Turk 2005; Fitzhugh, Phillips, and Gjesfeld 2011). As Captain Snow (1897:22) notes in his diary about the Kuril Ainu, “The Kurilsky inhabiting the central islands frequently shifted their quarters from one island to another. When the ‘flitting’ took place it was a matter of serious consideration. The weather had to be watched very closely both for storms and fogs. Should the latter set in when they were at sea, there was a great risk of them not being able to find their destination”.

The analysis of faunal remains provides evidence for the occupation of the archipelago minimally during the spring and summer seasons. As discussed above, many faunal remains

from the South-central region are Alcids, which include auklets, puffins and mares. These related species typically only spend the spring and early summer onshore, while spending the rest of the year offshore and dispersed into small groups (Harding et al. 2005; Golubova 2002). Albatrosses also comprise a significant portion of the South and South-central faunal assemblage, which similar to Alcids are typically only found on land during the spring and summer breeding season. Unfortunately, evidence for year-round occupation is currently limited as none of the taxa (or age classes) from the faunal assemblage are able to distinguish winter seasonality. However, the combination of mostly local pottery production, obsidian exchange, pit houses, and redundant resources from island to island broadly implies a more fixed residential patterns with occasional logistical movement for the trade and/or exchange of resources and information.

#### **4.2 Do biogeographical and ecological differences relate to regional differences in the occupation and cultural history of the archipelago?**

The results of our comparative analysis indicate differences in the faunal remains, lithic artifacts, ceramic artifacts and population histories of Kuril biogeographic regions. Broadly speaking, artifacts and faunal remains from the South region are consistent with biogeographical expectations as there is greater diversity in faunal taxa, lithic raw materials, lithic flake sizes, pottery decorations, and raw clay sources in this region.

The South-central and North-central regions also demonstrate broad consistency with biogeographical expectations. This can be identified in the faunal assemblages, which show these regions having lower diversity when accounting for both richness and evenness. Low diversity in the South-central region is largely driven by the higher abundances and richness of birds in the faunal assemblage. The North-central region has a slightly different pattern with a greater abundance of invertebrates and a lower abundance of birds, a pattern more similar to the North region. Overall, this pattern suggests a reduced diet breadth in the North-central region with opportunistic exploitation of birds and marine mammals, but more concentrated exploitation of specific fish and invertebrate resources.

Despite important similarities, important differences are also seen in the faunal assemblages of the South-central and North-central regions. One of the most significant discrepancies is the types of fish being exploited: the South-central region is largely characterized by greenling, while the North-central fish assemblage is dominated by Pacific cod (Table 1). This could indicate that people used different harvesting strategies and fishing locations in the two regions as greenling are often found nearshore in kelp beds and rocky shoreline, whereas cod tends to be found in deeper water closer to sandy sea beds. Alternatively, the differences may also relate to changes in water temperatures and the habitat conditions in the two regions. The northern Kuril straits are influenced by ocean waters flowing into the Sea of Okhotsk from the East Kamchatka Current and the Bering Sea Gyre. Pack ice also sometimes makes it south to the more northerly islands in winter (as it does the southernmost islands near Hokkaido because of the counter-clockwise circulation of sea ice in the Sea of Okhotsk). As a result, and compared to the South-central islands, water temperatures around the North and North-central islands may have been more optimal for Pacific cod. This possibility could be evaluated with a more detailed comparison of modern cod distributions and paleo-proxy evidence of water temperature in the past.

Our comparative analysis broadly indicates that differences in the archaeological remains from each region are connected to differences in biogeography and ecology. The South-central and North-central regions are characterized by lower ecological diversity and greater insularity compared to the South and North regions, and the archaeology shows these regions having lower faunal diversity, higher proportions of locally produced pottery, fewer obsidian artifacts, and smaller flake sizes. These archaeological similarities between the South-Central and North-Central make it even more interesting that the two regions have such different occupation histories. As illustrated by the paleodemography model (Fig 9) the South-central region was intensively occupied during both the Epi-Jomon and Okhotsk periods while the North-central region had much less Jomon and Epi-Jomon occupation compared to the later Okhotsk surge. Given that we are unable to characterize the faunal and artifact patterns by time period, the statistical differences noted may in fact capture distinctive cultural practices of each group. In other words, we interpret some of the differences discussed above as potentially indicative of differences in how Epi-Jomon and Okhotsk populations were engaging with the landscape and resources of each region. These results fit with growing evidence (Gjesfjeld 2019) that the Okhotsk and Epi-Jomon occupations of the Kuril archipelago were both socially and structurally dissimilar (Takase 2014; Fitzhugh 2019).

#### **4.3 Do more remote and ecologically precarious regions show more punctuated occupation histories compared to others?**

The ability to buffer variability in the environment is commonly recognized as an important feature of foraging communities, especially those living in marginal landscapes (Damm et al. 2019; Minc and Smith 1989; Halstead and O'Shea 1989). A common expectation is that communities living in more remote and ecologically precarious regions will be more vulnerable due to low species abundance and variety. Our comparison of archaeological remains and occupation histories between Kuril biogeographic regions enables us to comment broadly on the validity of this expectation. The paleodemography model discussed above (Fig 9) clearly shows a series of population booms and busts, one associated with the Epi-Jomon occupation and one associated with the Okhotsk occupation. The severity of the Epi-Jomon collapse is different between the South and South-central regions, with the more ecologically diverse South region showing more rapid decline and near complete abandonment by 1500 calBP compared to the less diverse South-central region. This may indicate that the cause of the collapse originated, not from ecological hardship, which should have affected the more remote and less ecologically diverse regions more, but from developments outside the archipelago. In contrast, the decline associated with the Okhotsk occupation shows a trend more consistent with ecological vulnerability. In this case, the southern islands show a more gradual decline in population density starting around 1100 calBP as compared to the precipitous, if somewhat later, declines in the South-central and North-central regions occurring between 800 and 550 calBP.

One hypothesis that emerges from our regional comparison is that population decline in the South region starting around 1100 calBP may have helped to fuel the population rise in the South-central and North-central regions around this same time period. This may be an outcome of migrants moving north, or a reduction in Okhotsk seasonal mobility or social networks to the south. Either scenario has the occupation of the South-central and North-central islands strongly



intensifying between 1100-800 calBP and potentially moving Okhotsk communities closer to the carrying capacity of these more ecologically precarious regions where they would be more vulnerable to unpredictable hazards. As discussed elsewhere (Fitzhugh et al. 2016), the ultimate cause for the dramatic decline in Kuril population starting around 800 calBP is still unclear, but it is likely a combination of events including changes in climate, social networks, political relationships, and possibly even epidemic diseases. Broadly speaking, we can suggest that remote and ecologically precarious regions may in fact demonstrate more punctuated changes in demography, but this is more likely to happen when communities are already at or near the ecological capacity of their landscape.

## 5. Conclusion

In this paper we have presented a comparative biogeographic analysis to better understand human resilience and adaptation in the Kuril Islands. Our approach is facilitated by the unique configuration of the Kuril Islands and the distinctive biogeographical differences that exist between regions. Overall, various lines of archaeological evidence are consistent with biogeographic expectations of greater ecological and human vulnerability in the more precarious South-central and North-central regions. The depressed ecological diversity and relative isolation of these regions likely posed greater risks to their settlement by small, maritime foraging communities. The archaeological record discussed here, and elsewhere (Fitzhugh, Phillips, and Gjesfeld 2011; Gjesfeld 2014; Fitzhugh et al. 2016), shows evidence of the adaptive strategies used by Kuril communities mitigate these risks. The strategies used by Kuril populations undoubtedly encouraged the settlement and occupation of the archipelago, but ultimately the scarcity and vulnerability of resources in combination with unpredictable social, economic and environmental changes made the Kuril Islands a challenging and risky place to live. Even so, the comparative, biogeographical analyses presented here helps also to direct our attention to social, economic, and cultural patterns operating at different spatial scales. These factors altered the occupation history of the archipelago in ways that are refracted through, but not determined, by biogeography and relative isolation. Teasing apart these more complex factors demands better chronological resolution over larger archaeological data sets from a range of sites throughout the archipelago. With opportunities for continued collaboration in archaeological research in the Kurils, we look forward to investigating these patterns further in ongoing and future research.

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## Supplemental Information

Two supplemental data tables (Table S1; Table S2) are provided. Table S1 provides additional information on the faunal remains discussed above including species names and abundances when available. Table S2 provides a regional, numeric summary of the faunal material grouped by taxonomic class.

## Data Accessibility

Radiocarbon dates used in the research were previously published in Fitzhugh et al. (2016), available at doi:10.1016/j.quaint.2016.02.003. Geochemical compositional data on ceramic artifacts are curated in the Digital Archaeological Record (tDAR) available here: doi:10.6067/XCV85M66NM. Additional data generated from the Kuril Biocomplexity Project including information on faunal remains can also be found curated in the tDAR project archive available here: doi:10.6067/XCV8BC40ZG.

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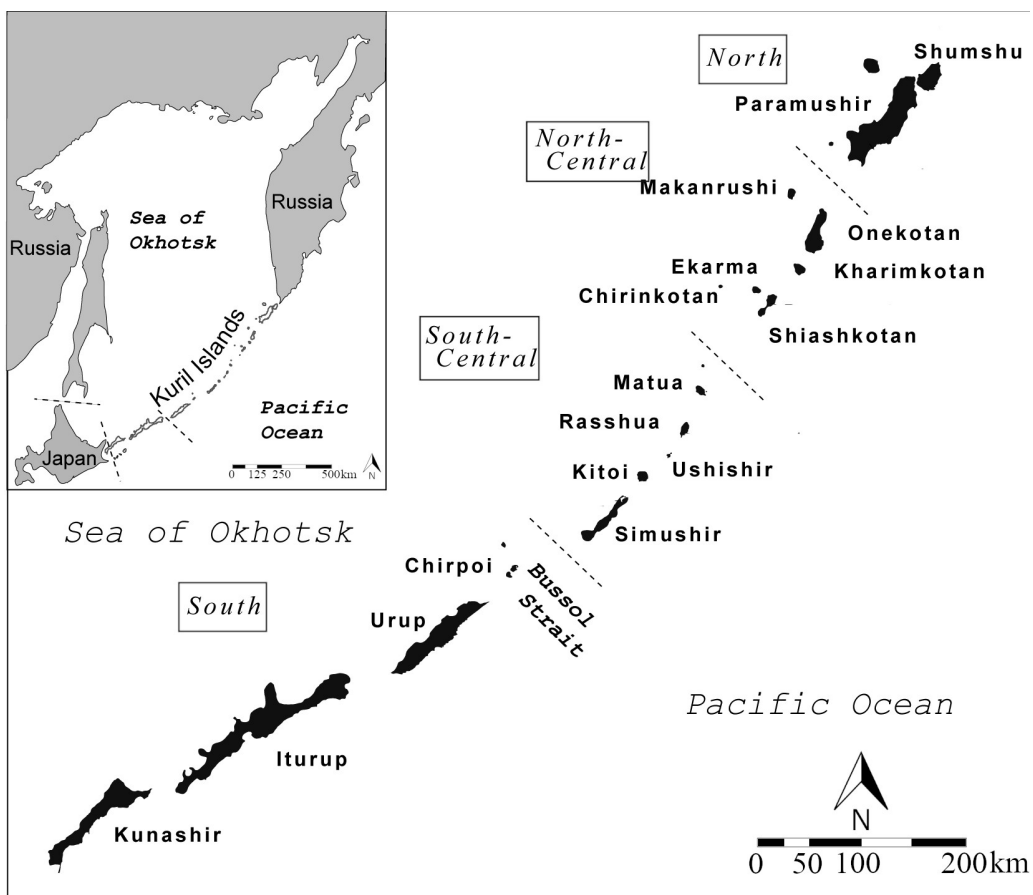


Figure 1



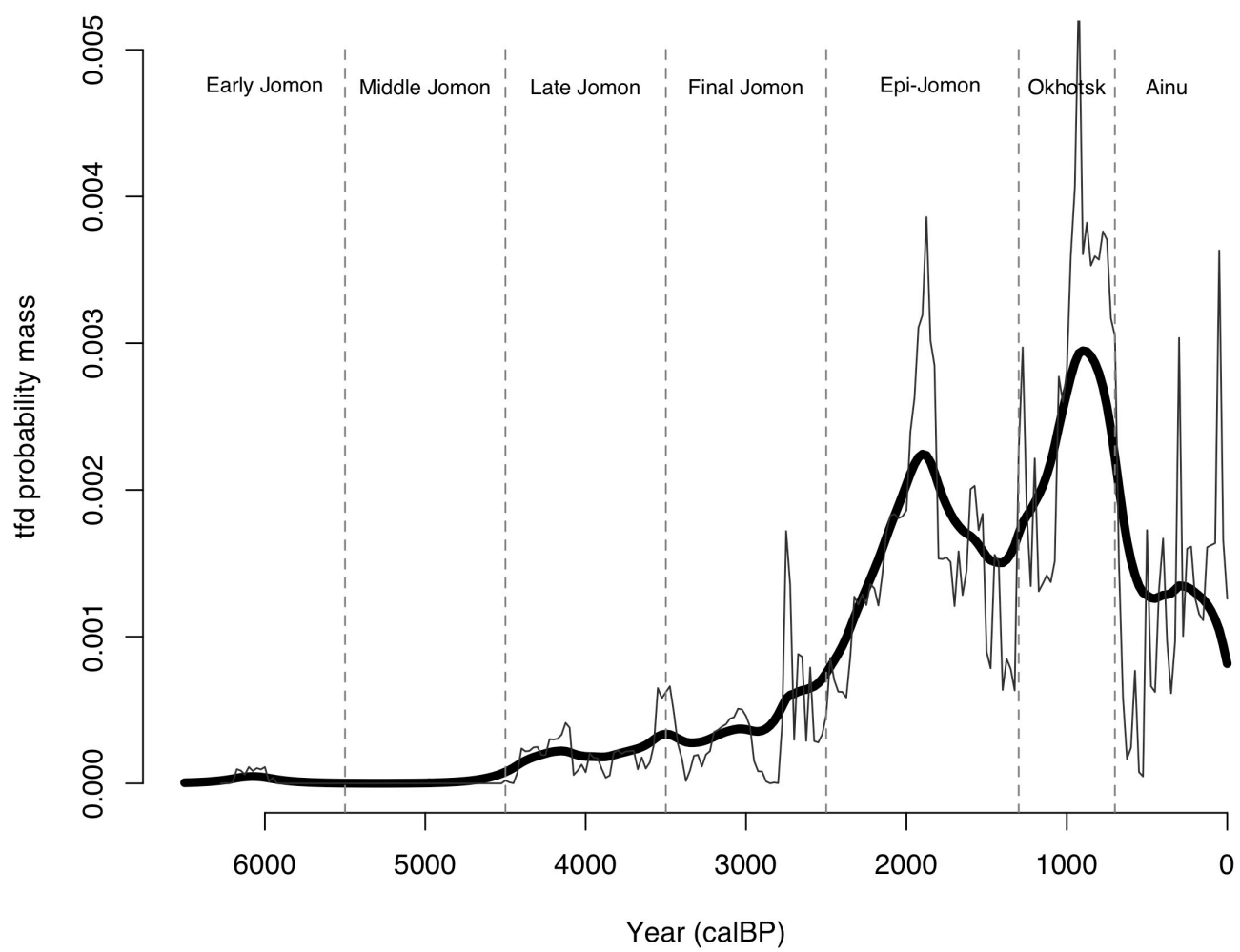


Figure 2

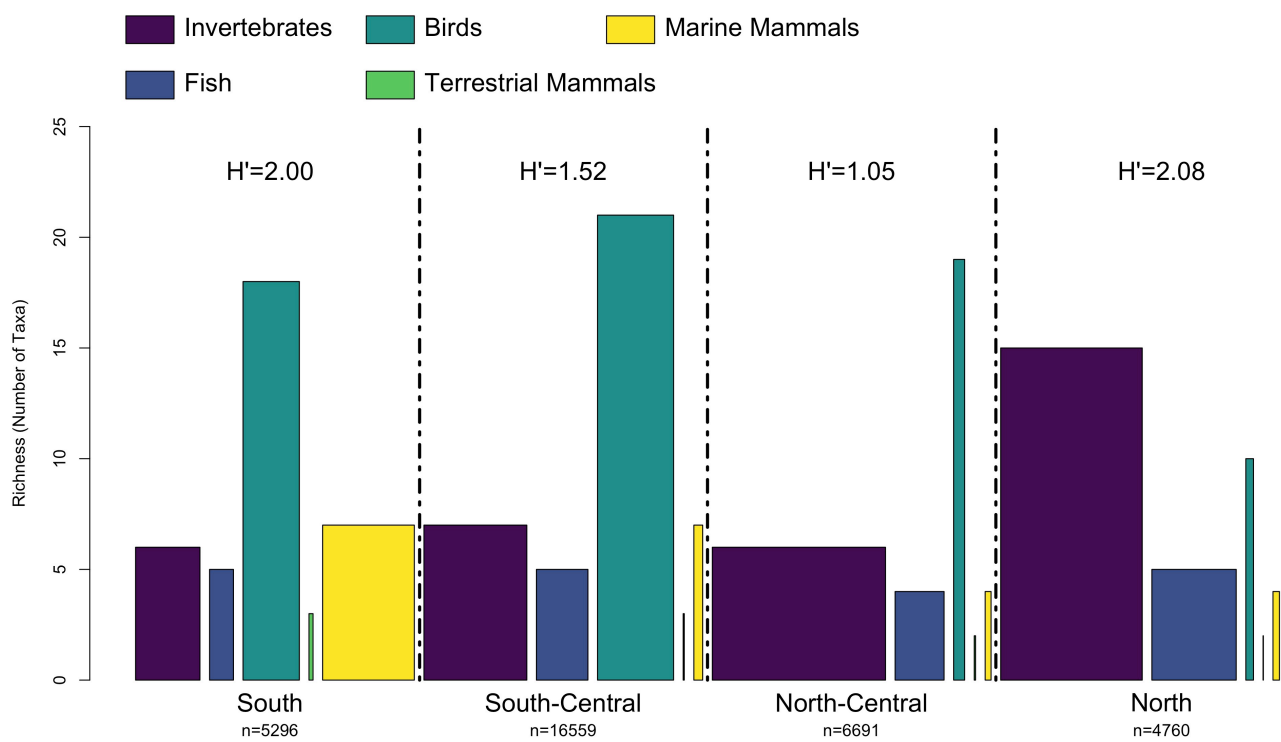


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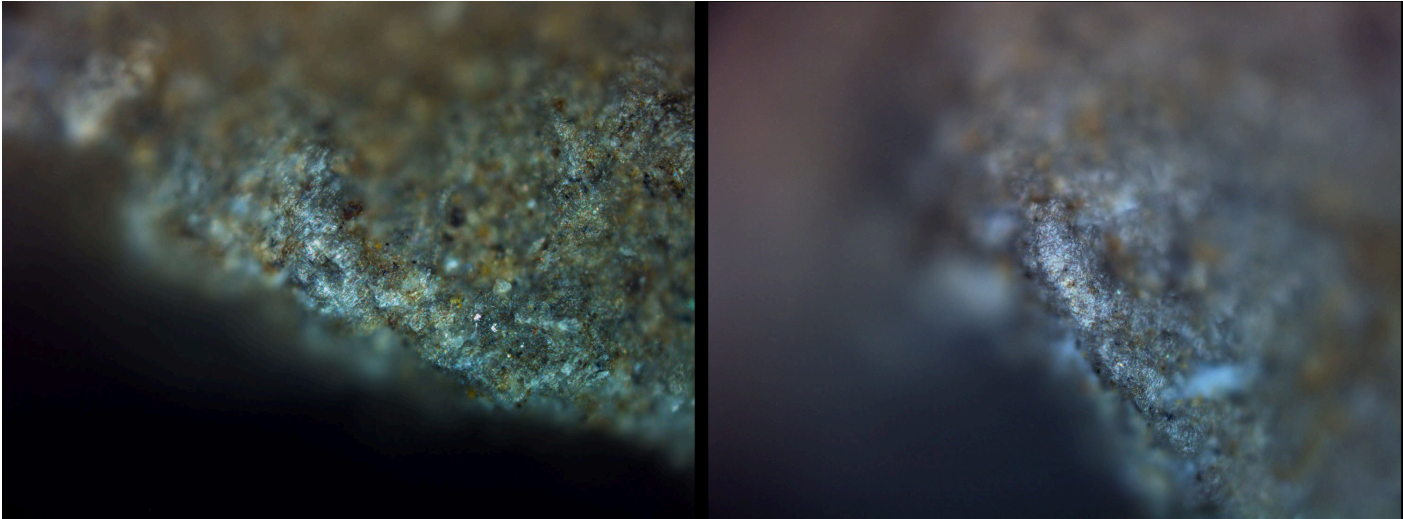


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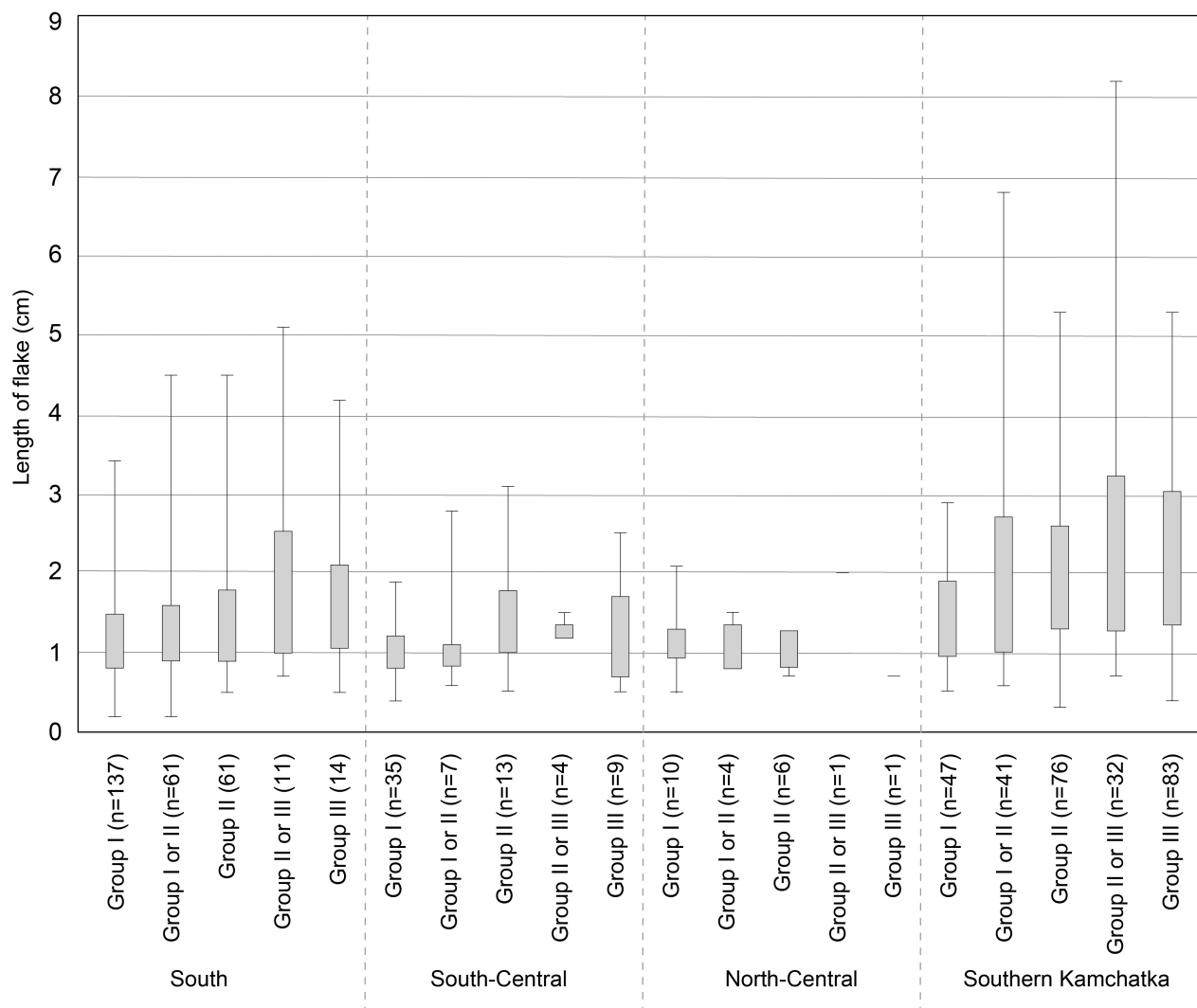


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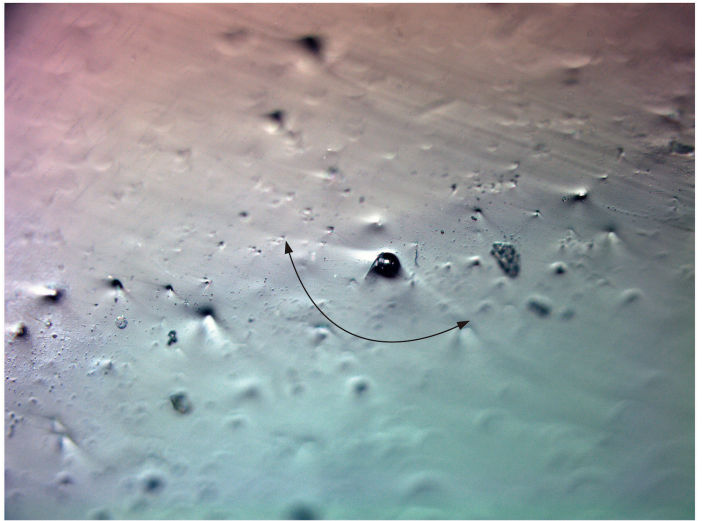
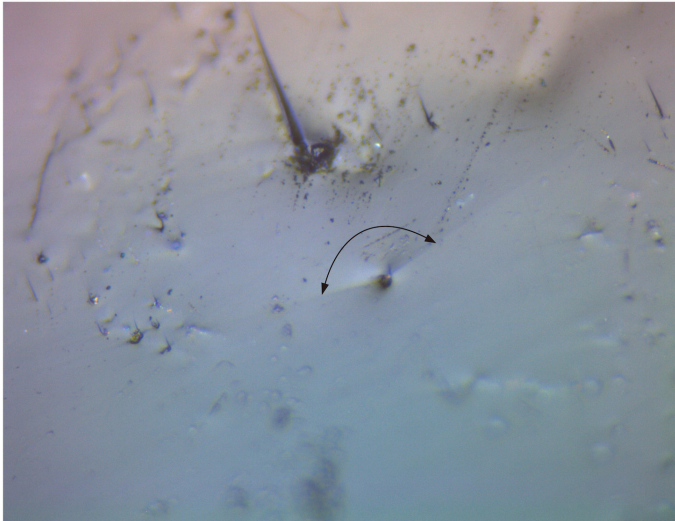


Figure 6



Figure 7

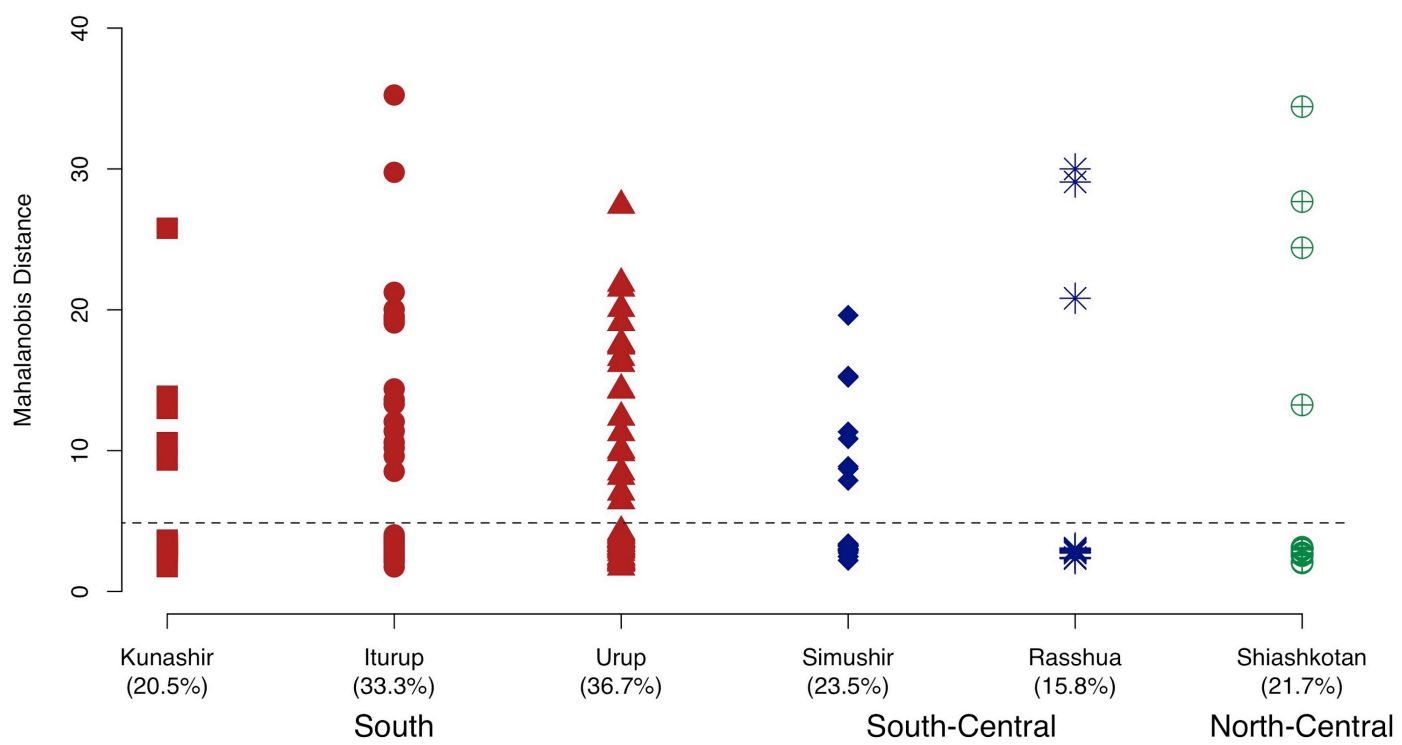


Figure 8



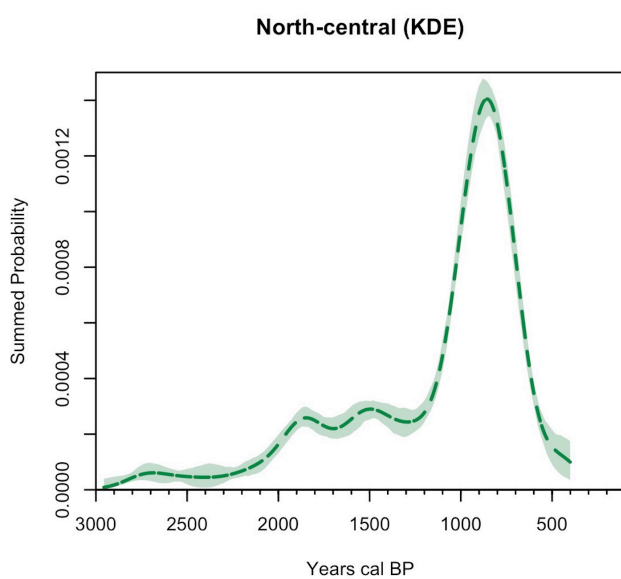
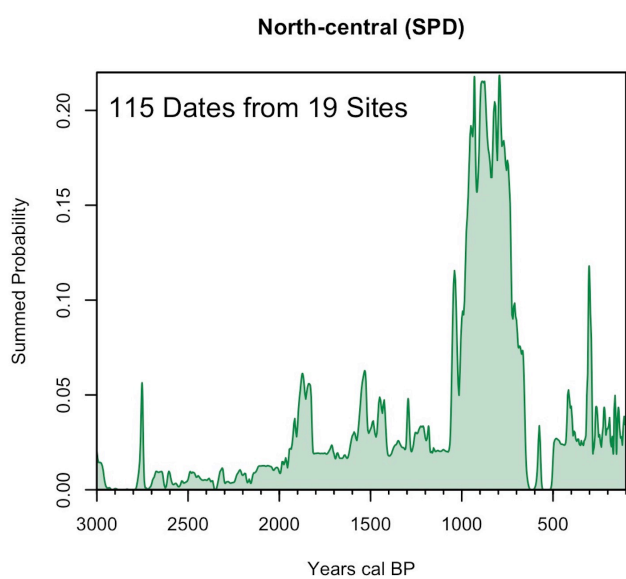
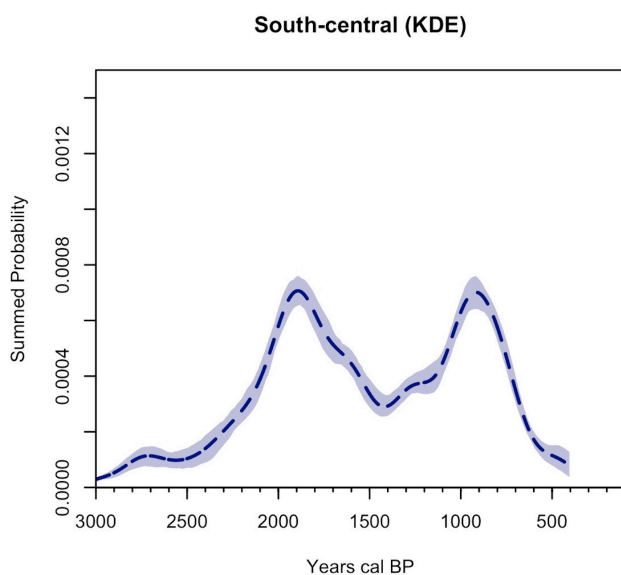
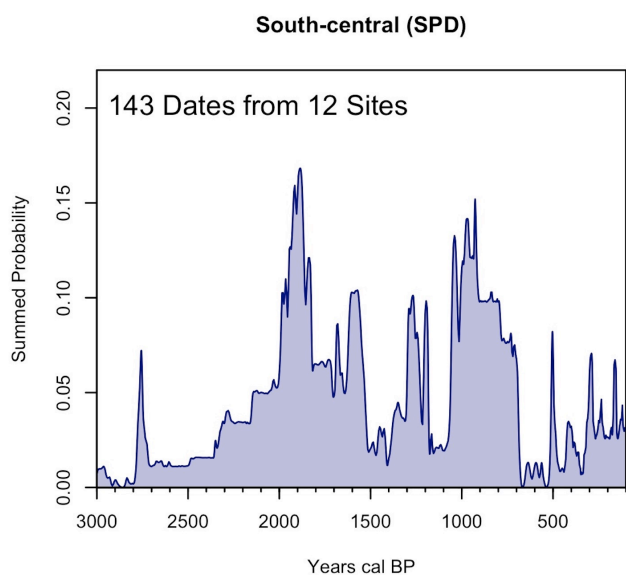
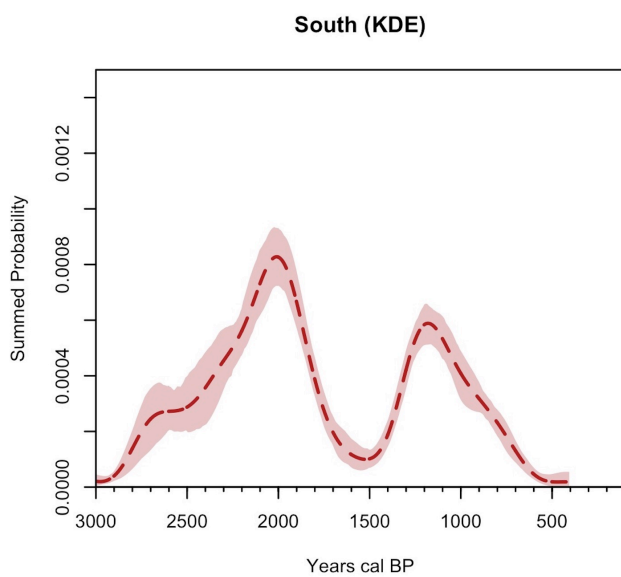
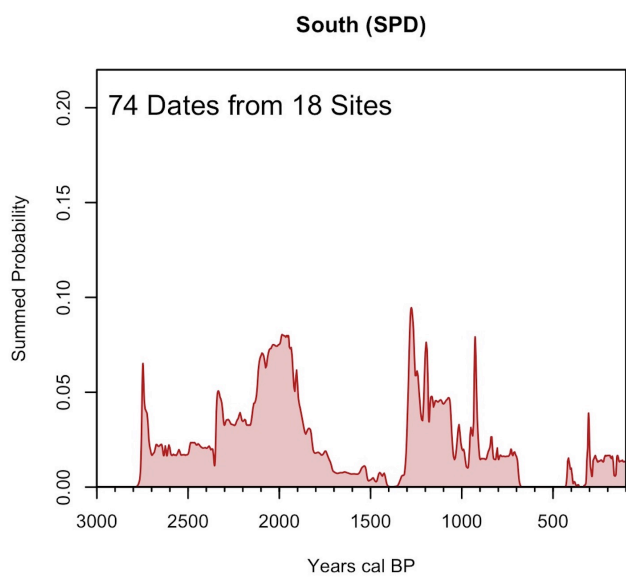


Figure 9



## Supplemental Information

Table 1. NISP values for each taxonomic group identified from the KBP faunal assemblage.

Taxonomic Group and Taxon		South	South-Central	North-Central	North
<b>INVERTEBRATES</b>					
	urchin	773	365	110	224
	barnacle	1	3	0	39
	Pectinidae	0	0	0	1
	Chiton	1	0	0	6
	Buccinum sp.	45	38	24	360
	limpet	0	3	2	9
	Nucella cf. canaliculata	0	0	0	3
	Nucella cf. lima	11	330	95	351
	Nucella sp.	0	0	0	44
	unident. whelk	15	194	5	1
	Littorina sp.	553	6135	4542	1173
	cf. Littorina sp.	20	2	11	0
	Gastropoda	3	12	1	1
	Gastropoda (unanalyzed)	1	1300	0	0
Gastropods (TOTAL)		1423	8382	4790	2212
	Clinocardium sp.	0	0	0	11
	Hiatella arctica	0	0	0	4
	Modiolus sp.	0	0	0	3
	Mya sp.	0	0	0	2
	Mytilis sp.	0	20	33	510
	Serripes sp.	0	0	0	63
	Bivalve	0	0	0	28
Bivalves (TOTAL)		0	20	33	621
<b>ALL INVERTEBRATES (TOTAL)</b>		<b>1423</b>	<b>8402</b>	<b>4823</b>	<b>2833</b>
<b>FISH</b>					
	Shark, cf. Lamniidae	15	1	0	0
Sharks (TOTAL)		15	1	0	0
	Salmonidae	7	24	0	907
Salmon (TOTAL)		7	24	0	907
	Hemilepidotus sp.	3	1	1	0
	Cottidae	224	5	3	2
Sculpins (TOTAL)		227	6	4	2
	Hexagrammos sp.	1	3514	48	18
	cf. Hexagrammos sp.	0	1	0	0
	Pleurogrammus monopterygius	0	0	20	0
	Hexagrammidae	211	0	44	13
Greenlings (TOTAL)		212	3515	112	31
	cf. Gadus sp.	20	0	1226	1
	Gadidae	45	1	21	665
Cod (TOTAL)		65	1	1247	666
	Pleuronectidae	0	0	0	65
Flatfish (TOTAL)		0	0	0	65
	unident. fish	81	233	608	201
	fish, not analyzed	1470	4681	796	4
Unidentified Fish (TOTAL)		1551	4914	1404	205
<b>ALL FISH (TOTAL)</b>		<b>2077</b>	<b>8461</b>	<b>2767</b>	<b>1876</b>
<b>BIRDS</b>					
	Gavia arctica/pacifica	4	0	1	0
	Gavia immer/adamsi	4	0	0	0
	Gavia sp.	1	2	4	4
	cf. Gavia sp.	1	0	0	0
	Podicepsidae	4	0	0	1
Loons and Grebes (TOTAL)		14	2	5	5
	Phoebastria cf. albatrus	1	0	0	0
	Phoebastria cf. nigripes	1	0	0	0
	Phoebastria sp.	311	1242	6	2
	cf. Phoebastria sp.	1	20	0	0
Albatrosses (TOTAL)		314	1262	6	2
	Puffinus sp.	21	1	1	0

	Fulmarus glacialis	38	500	86	0
	cf. Fulmarus glacialis	6	78	9	0
	Procellariidae	3	2	0	0
	Oceanodroma sp.	2	28	1	0
Tubenouts (TOTAL)		70	609	97	0
	Phalacrocorax cf. pelagicus	3	2	1	0
	Phalacrocorax sp.	299	169	61	73
	cf. Phalacrocorax sp.	7	8	2	3
Cormorants (TOTAL)		309	179	64	76
	Aethia cristatella	0	4	0	0
	Aethia cf. cristatella	0	0	1	0
	Aethia pusilla	0	3	0	0
	Aethia cf. pusilla	0	3	0	0
	Aethia pygmaea	0	4	0	0
	Aethia sp.	8	1633	19	0
	Alcidae, cf. Aethia sp.	1	9	0	0
	Cephus sp.	0	2	0	0
	Alcidae, cf. Cephus sp.	0	0	0	1
	Fratercula cf. cirrhata	0	1	0	0
	Fratercula sp.	29	813	28	7
	Alcidae, cf. Fratercula sp.	3	54	3	0
	Uria cf. lomvia	1	1	0	0
	Alcidae, cf. Uria sp.	4	15	1	1
	Uria sp.	84	150	6	6
	Alcidae	6	107	1	3
	cf. Alcidae	0	7	0	0
	Alcidae, large	0	1	0	0
Auklets, puffins, and murres (TOTAL)		136	2807	59	18
	Anatidae, cf. Clangula hyemalis	0	1	0	0
	Anatidae, cf. Histrionicus histrionicus	0	1	1	0
	Anatidae, cf. Somateria sp.	1	0	1	0
	Anatidae, duck	31	77	13	25
	cf. Anatidae, small duck	0	0	0	1
	cf. Anatidae, duck	0	2	0	0
	Anatidae, goose	7	94	7	0
	Anatidae, goose/duck	0	2	0	0
	cf. Anatidae, goose	0	11	0	0
	Cygnus sp.	0	0	1	0
	Anatidae, goose/swan	2	0	0	0
	Anatidae, large	0	0	4	0
	Anatidae	1	44	6	0
Ducks, geese, and swans (TOTAL)		42	232	33	26
	Larus cf. schistisagus	0	1	0	0
	Larus sp.	34	58	6	19
	cf. Larus sp.	1	0	0	2
	Rissa sp.	1	7	2	0
	cf. Rissa sp.	3	0	1	0
Gulls (TOTAL)		39	66	9	21
	Haliaeetus sp.	290	45	2	0
	Falco peregrinus	0	1	0	0
	cf. Haliaeetus sp.	8	2	0	0
	Strigidae	0	1	5	0
	Strigidae, cf. Nyctea scandiaca	0	0	3	0
	cf. Strigidae	0	1	0	0
	unident. raptor	14	22	0	0
Raptors (TOTAL)		312	72	10	0
	Corvus cf. machrorhynchos	4	2	0	0
	cf. Corvidae, Corvus sp.	0	0	0	1
	Corvus sp.	1	9	11	2
	unident. Passerine	0	12	0	0
Songbirds (TOTAL)		5	23	11	3
	Lagopus sp.	0	0	11	0
Ptarmigan (TOTAL)		0	0	11	0
	unident. bird	388	2083	130	76
	unident. bird (large)	0	4	0	0

	unident. bird (medium)	12	41	2	1
	unident. bird (pending)	31	140	1	15
	unident. bird (small)	0	0	1	0
Unidentified Birds (TOTAL)		431	2268	134	92
<b>ALL BIRDS (TOTAL)</b>		<b>1672</b>	<b>7520</b>	<b>439</b>	<b>243</b>

# MAMMALS

	Canis familiaris	17	3	3	2
	Canidae, cf. Canis familiaris	3	1	0	0
	Vulpes vulpes	38	49	31	2
	Canidae, cf. Vulpes vulpes	8	3	1	2
	Canidae	7	14	2	0
	Carnivora, cf. Canidae	1	0	0	0
Dogs and foxes (TOTAL)		74	70	37	6
	Enhydra lutris	200	30	10	29
	Carnivora, cf. Enhydra lutris	7	2	5	2
	Ursus arctos	9	0	0	0
	Carnivora	2	2	0	0
Other Carnivores (TOTAL)		218	34	15	31
	Callorhinus ursinus	47	114	26	1
	cf. Callorhinus ursinus	8	9	6	0
	Eumetopias jubatus	142	62	40	20
	cf. Eumetopias jubatus	7	2	2	2
	Zalophus japonicus	1	1	0	0
	Otariidae	62	17	13	4
	Pinniped, cf. Otariidae	4	0	1	3
	Otariidae (Cu/Ej)	16	11	5	1
	Otariinae	2	0	0	0
Fur seals and sea lions (TOTAL)		289	216	93	31
	Phoca vitulina	12	5	4	2
	Phocidae, cf. Phoca vitulina	1	2	0	0
	Phoca vitulina/largha	4	0	0	0
	Phoca sp.	285	261	42	54
	Phocidae, cf. Phoca sp.	23	7	3	3
	Pusa hispida	1	1	0	0
	Phocidae, cf. Pusa hispida	2	0	0	0
	Phocidae	147	10	0	0
	Pinniped, cf. Phocidae	12	1	0	2
True seals (TOTAL)		487	287	49	61
	Pinniped	67	58	7	5
	Bos taurus	3	0	0	0
	Sus scrofa	1	0	0	0
	Artiodactyla	5	1	0	0
Artiodactyls (TOTAL)		9	1	0	0
	Delphinidae, cf. Pseudorca crassidens	1	0	0	0
	Phocoenidae	962	15	0	0
	cf. Phocoenidae	7	1	0	0
Dolphins and porpoises (TOTAL)		970	16	0	0
	Odontocete (large)	1	0	0	0
	Cetacea	565	75	24	10
	cf. Cetacea	12	3	1	1
	Cetacea (medium)	0	1	0	1
Other Cetaceans (TOTAL)		578	79	25	12
	unident. mammal	1905	681	390	166
	unident. mammal (small)	0	0	0	3
	unident. mammal (medium)	210	0	12	0
	unident. mammal (large)	68	3	4	1
	unident. mammal (marine)	0	1	0	0
	mammal, not ID-ed	6	120	0	0
Unidentified Mammals (TOTAL)		2189	805	406	170
<b>ALL MAMMALS (TOTAL)</b>		<b>4881</b>	<b>1566</b>	<b>632</b>	<b>316</b>
	unident. vertebrate	52	136	140	15
Unidentified Vertebrates (TOTAL)		52	136	140	15

Table 2. Table of richness (number of taxa) and NISP (number of identified specimens) for faunal remains that could be identified to their taxonomic group. A Shannon-Weaver diversity index is also included, which provides a measure of diversity accounting for both the richness and evenness of the faunal assemblages.

Region	Taxonomic Group	Number of Taxa	NISP	Shannon Diversity
South	Invertebrates	6	1419	0.85
	Fish	5	526	1.27
	Birds	18	1241	1.43
	Terrestrial Mammals	3	90	0.93
	Marine Mammals	7	2020	0.61
	<b>Totals</b>	<b>39</b>	<b>5296</b>	<b>2</b>
South-central	Invertebrates	7	7090	0.46
	Fish	5	3547	0.05
	Birds	21	5240	1.04
	Terrestrial Mammals	3	73	0.31
	Marine Mammals	7	609	1.27
	<b>Totals</b>	<b>43</b>	<b>16559</b>	<b>1.52</b>
North-central	Invertebrates	6	4822	0.28
	Fish	4	1363	0.24
	Birds	19	305	1.9
	Terrestrial Mammals	2	37	0.3
	Marine Mammals	4	164	1.12
	<b>Totals</b>	<b>35</b>	<b>6691</b>	<b>1.05</b>
North	Invertebrates	15	2804	1.64
	Fish	5	1671	0.35
	Birds	10	151	1.47
	Terrestrial Mammals	2	6	0.69
	Marine Mammals	4	128	1.89
	<b>Totals</b>	<b>36</b>	<b>4760</b>	<b>2.08</b>